Effect of floral nectar, water, and feeding frequency on *Cotesia glomerata* longevity

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Abstract This study examined how water, sucrose, and frequency of nectar availability affects the longevity of the parasitoid *Cotesia glomerata* (L.) (Hymenoptera: Braconidae). Under standard laboratory conditions, water did not extend longevity in the absence of sugar in three out of four comparisons, nor did it extend longevity with access to nectar. *Cotesia glomerata* lived 2–3 days when given water or nothing, 8–15 days when given buckwheat (*Fagopyrum esculentum* Moench) nectar daily with or without water, and 23–26 days when given a 50% sucrose solution. The lifespan of *C. glomerata* fed flowers every other day was one-third shorter than that of *C. glomerata* fed flowers every day, but this difference was not statistically significantly. Only minimal benefits occurred when flowers were given every 3 days.

Keywords Braconidae · Hydration · Hymenoptera · Meal frequency · Parasitoid · Rearing · Sugar feeding

Introduction

Cotesia glomerata (L.) (Hymenoptera: Braconidae) is an endoparasitoid of *Pieris rapae* (L.) and *Pieris brassiceae* (L.) (Lepidoptera: Pieridae) in Europe, North America, Asia, and Australia. This parasitoid does not host feed but is strongly stimulated to feed on sucrose, glucose, and fructose (Wäckers 1999), and feeding on these sugars increases their longevity 15-fold (Wäckers 2001). Also, feeding on various floral nectars, especially annual buckwheat, *Fagopyrum esculentum* Moench

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(Polygonaceae), greatly extends the lifespan of *C. glomerata* (Winkler 2005). Starved *C. glomerata* unable to fly later recover and fly within an hour of feeding on fructose, glucose, sucrose, and melezitose (Hausmann et al. 2005). A diet of dill nectar or honey enables *C. glomerata* females to fly longer distances and for a longer duration than females given only water (Wanner et al. 2006a).

While numerous studies have examined sugar feeding among hymenopteran and dipteran parasitoids, the role of water and feeding frequency has not been examined as often. For some parasitoid species, sugar-starved individuals live longer with access to water (Dyer and Landis, 1996; Sengonca et al. 1994; Fadamiro et al. 2005; Krugner et al. 2005). Providing sugar in water solution is far more beneficial than solid sugar with water (Wäckers 2000; Pinto et al. 2005). Recently, the optimal frequency of feeding, and lifespan gain from one sugar meal/day has been examined for various parasitoids (Siekmann et al. 2001; Azzouz et al. 2004; Fadamiro et al. 2005). A 100 μ g intake of sucrose extends the lifespan of C. glomerata by 50 h (Hausmann et al. 2005). Interestingly, the lifespan of Macrocentrus grandii (Goidanich) was 3 days longer when sucrose was given every other day rather than daily, but this difference was not statistically significant (Fadamiro and Heimpel 2001). Knowing the water and sugar-feeding frequency requirements of a parasitoid may help improve mass rearing and habitat manipulation programs. Our objectives were to determine the role of water, and the frequency of floral nectar availability on the longevity of C. glomerata.

Materials and methods

Cotesia glomerata were reared from field-collected P. rapae larvae fed cabbage in the laboratory. Each newly-emerged wasp was placed in a separate 100 × 15 mm Petri dish. In experiment 1, wasps emerging from 7-13 October 2000 were given ad libitum: 50% sucrose solution (w/w), buckwheat flowers, water, or no water (female n = 26, 30, 28, 26, male n = 12, 12, 12, 14, respectively). Sucrose and water were dispensed in 0.6 ml microcentrifuge tubes plugged with cotton. Flower stems were similarly inserted into a water-filled tube along with a cotton plug, and a dry tube plugged with cotton served as the no-water control. Flowers were replaced every other day and sucrose was replaced weekly. In a second experiment, wasps emerging from 13 October to 12 November 2000 were given: fresh buckwheat flowers daily, alternating fresh flowers 1 day and water the next day, alternating fresh flowers every 3 days and water the other 2 days, fresh flowers daily without access to water, water, or no water (female n = 9, 17, 18, 17, 17, 20, male n = 29, 23, 21, 23, 20, 16,respectively). Flowers were inserted into water-filled tubes with cotton plugs where wasps could contact the wet cotton except for the 'flowers daily no water' treatment where parafilm was wrapped around the floral stem covering the wet cotton. Wasps were kept in a growth chamber at 16L: 8D, 26°C, 75% r.h., checked daily for mortality, and sexed under the microscope upon death. Survival curves of females and males were separately tested for the effect of diet using a Wilcoxon test (PROC PHREG, SAS Institute 2001). For multiple comparisons, each pair of curves was tested with an adjusted sequential Bonferroni α (Rice 1989). All P-values were ranked from lowest to highest $(P_1, P_2, P_i \dots P_k, where k$ is the number of tests) and tested sequentially and considered significant if $P_i < \alpha/(1+k-i)$, where $\alpha = 0.05$.



Results and discussion

In the absence of sugar, water did not extend lifespan for females in experiment 1 (no water versus water, Fig 1a), and females and males in experiment 2 (Fig 2a,b). Males in experiment 1 survived longer with water than without water (Fig 1b) indicating that *C. glomerata* may sometimes require water for hydration. Other species of sugar-starved parasitoids did not benefit from access to water (Idris and Grafius 1995; Leatemia et al. 1995). However, water has sometimes benefitted starved parasitoids under higher temperatures and low humidity (Dyer and Landis 1996) which may be expected in the field.

Results of experiment two indicated that access to water did not significantly increase the longevity of females or males in the presence of floral nectar (flower daily versus flower daily no water, (Fig 2a,b). This may occur since buckwheat nectar has adequate water content, the sugar content of buckwheat is 13–34% of total

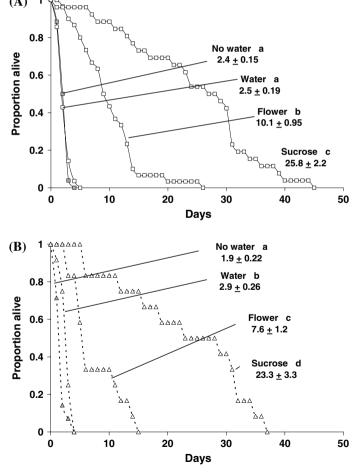
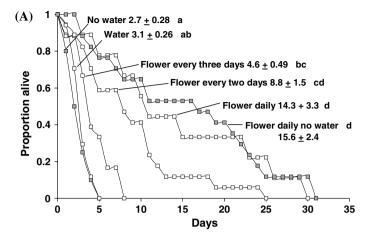


Fig. 1 Survivorship curves and lifespan (means \pm SEM) of *C. glomerata* among diet treatments in experiment 1: (A) females treatment effect Wilcoxon $\chi^2 = 89.3$, df = 3, P < 0.0001, and (B) males $\chi^2 = 49.6$, df = 3, P < 0.0001. Shaded shapes indicate treatments without water





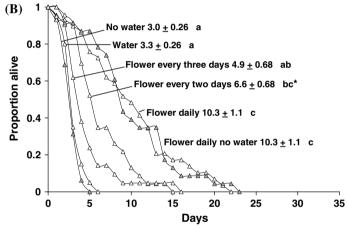


Fig. 2 Survivorship curves and lifespan (means \pm SEM) of *C. glomerata* among diet treatments in experiment 2: (A) females $\chi^2 = 50.8$, df = 5, P < 0.0001, and (B) males $\chi^2 = 70.4$, df = 5, P < 0.0001. * Pairwise comparison between flower every 2 days versus flower daily no water P = 0.0078 where $\alpha_{\rm adj} = 0.0071$, and flower every 2 days versus flower daily P = 0.0093 where $\alpha_{\rm adj} = 0.0083$

weight (Lee and Heimpel 2003). In contrast, pure honey has a sugar content of ~81% of total weight (National Honey Board 2006), and the addition of water is beneficial to parasitoids when provided with honey. Parasitoids feeding on pure honey compared to 50% diluted honey required longer feeding times (Siekmann et al. 2001), and had reduced lifespans (Munniapan et al. 2004). This may have occurred if parasitoids had difficulty feeding on highly viscous honey, and the resulting high osmotic pressure in the gut. While diluting concentrated sugars in water is helpful to parasitoids, it is still unclear whether having separate water sources will aid sugar uptake and digestion. This requires testing parasitoids given concentrated sugar sources with and without access to a separate water source.

Sucrose extended longevity significantly more than did buckwheat flowers for both sexes in experiment 1 (Fig 1a,b). The composition of buckwheat nectar is primarily sucrose, glucose and fructose (Wäckers et al. 2006), and well utilized by *C. glomerata* (Wäckers 2001). Greater longevity on sucrose was possibly due to the



fact that cut buckwheat flowers produce a limited amount of nectar since flowers were replaced only every other day in the first experiment.

Lastly, feeding frequency affected longevity in experiment 2; wasps lived 10--15 days when given fresh flowers daily, 7–9 days when given flowers every 2 days, and 4–5 days when given flowers every 3 days (Fig 2a,b). Daily feeding on floral nectar appeared optimal since feeding every 2 days appeared to shorten lifespan by about one-third. These differences were not significant, but pairwise comparisons among males given flowers daily versus every 2 days had P-values that were just 0.0007 and 0.001 above the significant α -level (Fig 2b). Feeding every 3 days was not sufficient because C. glomerata died as quickly as starved wasps in three of four comparisons (flower every 3 days versus water or control, Fig 2a,b). Similary, Aphidius ervi (Haliday) died quickly when fed every 3 days, and even required feeding twice a day, as feeding once per day decreased lifespan by one-sixth (Azzouz et al., 2004).

These results suggest that habitat manipulation and mass rearing programs should provide a continuous supply of sugar or nectars to parasitoids, as infrequent feeding opportunities will have limited benefits. The importance of sugar feeding could be greater in the field than anticipated from laboratory tests where parasitoids are less active and maintained under moderate conditions (Steppuhn and Wäckers 2004; Winkler et al. 2006). Beyond the physiological benefits to *C. glomerata*, three studies provide insight on whether nectar sources subsequently enhance parasitism by C. glomerata on Pieris larvae in cabbage fields. As expected, Al-Doghairi and Cranshaw (2004) found that floral plantings of the commercial "Good Bug Blend" significantly increased combined parasitism levels by C. glomerata and the tachinid Lespesia sp. on P. rapae larvae by 21.8% compared to the control. Also, buckwheat plantings increased parasitism levels by 12.9% though not significantly. Unexpectedly, Lee and Heimpel (2005) found no overall effect of buckwheat over 4 years in cabbage fields. This was possibly because a honeydew-producing aphid had surrounded experimental plots in the 2nd-4th years, and confounded the effects of buckwheat. However, the effect of treatment x year was marginally significant (P = 0.07). In the first year before surrounding fields became established with another sugar source, C. glomerata parasitism rates were slightly higher in buckwheat than control plots by 4.1%. Recently, Wanner et al. (2006b) tracked the oviposition of ⁴⁴Ca marked C. glomerata, and found random parasitism on P. brassicae on cabbage near flowering and non-flowering borders. No clear spatial trends in parasitism appeared because females were able to disperse throughout the fields, over 1225 m². The high dispersal ability of C. glomerata could also explain why parasitism rates were not substantially different between buckwheat and control plots in Lee and Heimpel (2005) since plots were separated by 67 m in the first year study.

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